werden erwogen: 1) Erscheinung der Extrazähne als Folge einer übermäßigen Entwicklung der Schädelgröße; 2) Atavismus; 3) Persistenz des dritten Milchprämolaren bei Erscheinen des Dauerzahnes; 4) Wachstumsstörungen, die zur Verdoppelung eines Zahnkeimes führen. Die erste Hypothese wird verworfen, da alle Einzelindividuen eine arttypische Größe haben. Kein fossiler Hinweis unterstützt auch die zweite. Die Morphologie der beobachteten Zähne unterstützt auch die dritte nicht, da es sich um Zähne des Dauergebisses handelt. Schließlich ist es schwierig, Beweise gegen oder zugunsten der vierten Hypothese zu finden, da keine Informationen vorhanden sind, über die Entwicklung der Zähne bei den bearbeiteten Museumsexemplaren.

# References

- ALLEN, J. A. (1901): A preliminary study of the north American opossums of the genus *Didelphis*. Bull. Am. Mus. Nat. Hist. 14, 149–188.
- ARCHER, M. (1974): The development of premolar and molar crowns of *Antechinus flavipes* (Marsupialia, Dasyuridae) and the significance of cusp ontogeny in mammalian teeth. J. R. Soc. West. Austr. 57, 118–125.
- BARBOUR, R. A. (1977): Anatomy of marsupials. In: The Biology of Marsupials. Ed. by B. STONEHOUSE and D. GILMORE. London: Macmillan Press. Pp. 237–272.
- BERKOVITZ, B. K. B. (1978): Tooth ontogeny in *Didelphis virginiana* (Marsupialia: Didelphidae). Austr. J. Zool. 26, 61–68.
- BUTLER, P. M. (1939): Studies of the mammalian dentition. Differentiation of the post-canine dentition. Proc. Zool. Soc. Lond. (B) **109**, 1–36.
- DREHMER, C. J.; FERIGOLO, J. (1996): Anomalias e patologias dentárias em Arctocephalus G. Saint Hilaire and Cuvier (Pinnipedia, Otariidae) da costa do Rio Grande do Sul. Rev. Brasil. Zool. 13, 857–865.
- FELDHAMER, G. A.; STOBER, T. L. (1993): Dental anomalies in five species of North American shrews. Mammalia **57**, 115–121.
- FOWLE, C. D.; PASSMORE, R. C. (1948): A supernumerary incisor in the white-tailed deer. J. Mammalogy 29, 301.
- GOODWIN, H. T. (1998): Supernumerary teeth in Pleistocene, recent, and hybrid individuals of the *Spermophilus richardsonii* complex (Sciuridae). J. Mammalogy **79**, 1161–1169.
- HERSHKOVITZ, P. (1992): The South American gracile mouse opossums, genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notes on general morphology and relationships. Fieldiana: Zoology **70**, 1–56.
- HERSHKOVITZ, P. (1997): Composition of the family Didelphidae Gray, 1821 (Didelphoidea: Marsupialia), with a review of the morphol-

ogy and behavior of the included four-eyed pouched opossums of the genus *Philander* Tiedemann, 1808. Fieldiana: Zoology **86**, 1– 103.

- HOOPER, E. T. (1946): Extra teeth in shrews, J. Mammalogy 27, 394.
- KVAM, T. (1985): Supernumerary teeth in the European lynx, *Lynx lynx lynx*, and their evolutionary significance. J. Zool. (London) **206**, 17–22.
- KRUTZSCH, P. H. (1953): Supernumerary molars in the jumping mouse (*Zapus princeps*). J. Mammalogy 34, 265–266.
- LONG, C. A.; LONG, C. F. (1965): Dental abnormalities in North American badgers, genus *Taxidea*. Trans. Kansas Acad. Sci. 68, 145–155.
- MECH, L. D.; FRENZEL, L. D. JR.; KARNS, P. D.; KUEHN, D. W. (1970): Mandibular dental anomalies in white-tailed deer from Minnesota. J. Mammalogy 51, 804–806.
- PEKELHARING, C. J. (1968): Molar duplication in red deer and wapiti. J. Mammalogy **49**, 524– 526
- REIG, O. A.; KIRSCH, J. A. W.; MARSHALL, L. G. (1987): Systematic relationships of the living and Cenozoic American "opossum-like" marsupials (Suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In: Possums and Opossums: Studies in Evolution. Ed. by M. ARCHER. Sydney, Australia: Surrey Beatty and Sons and The Royal Zoological Society of New; South Wales. Pp. 1–89.
- STEELE, D. G.; PARAMA, W. D. (1979): Supernumerary teeth in moose and variations in tooth number in north american cervidae. J. Mammalogy 60, 852–854.
- TAKAHASHI, F. (1974): Ocorrência de poliodontia em *Didelphis* L. 1758 e sua possível correlação a uma forma ancestral. An. Acad. Brasil. Ciênc. **46**, 283–285.
- THENIUS, E. (1989): Zähne und Gebiß der Säugetiere. In: Handbuch der Zoologie. Vol. 8

Mammalia Part 56. Ed by J. NIETHAMMER, H. SCHLIEMANN, and D. STARCK. Berlin, New York: Walter de Gruyter.

- TRIBE, C. J. (1990): Dental age classes in *Marmosa* incana and other didelphoids. J. Mammalogy 71, 566–569.
- van Valen, L. (1962): Growth fields in the dentition of *Peromyscus*. Evolution **16**, 272–277.
- VAN VALEN, L. (1964): Nature of the supernumerary molars of Otocyon. J. Mammalogy 45, 284–286.

#### Authors' addresses:

DIEGO ASTÚA DE MORAES, Departmento de Zoologia, Universidade de São Paulo. C.P. 11461, 05422-970, São Paulo, SP, Brasil,

(e-mail: dmoraes@ib.usp.br), BERNARDO LEMOS and RUI CERQUEIRA, Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro. C.P. 68020. 21941-590, Rio de Janeiro, RJ, Brasil.



Zeitschrift für Säugetierkunde

# **Original investigation**

# A habitat analysis of badger (*Meles meles* L.) setts in a semi-natural forest

By TATJANA C. GOOD, KARIN HINDENLANG, S. IMFELD, and B. NIEVERGELT

Wildlife Research and Conservation Biology, Zoological Institute, University of Zurich, Zurich, Switzerland and Spatial Data Handling Division, Geographical Institute, University of Zurich, Zurich, Switzerland

Receipt of Ms. 27. 07. 2000 Acceptance of Ms. 22. 12. 2000

# Abstract

We studied the size, distribution and habitat characteristics of badger (Meles meles L.) setts in a largely forested area near the city of Zurich, Switzerland. The distribution of the setts was non-random, as revealed by testing nearest neighbour distances. To evaluate the habitat characteristics that determine sett locations, different parameter categories describing topography, vegetation cover and structure of the forest habitat were analysed with a multiple regression analysis and with a digital terrain model of the forest using a Geographical Information System (GIS). Preferred sett sites were the convex slopes with an inclination of 20-40°. These sites are well drained and offer many opportunities for digging entrances and tunnels, and thus gives the badger the option to leave the sett from several directions. Ideal sett sites were found above 600 metres a.s.l., closer to the forest boundary and adjoining agricultural zones than the random points. These sett sites probably guarantee access to a good food supply year-round and allow badgers to adapt their foraging behaviour to seasonal changes in food availability both within the mixed forest stands and in the agricultural fields and meadows outside the forest. Setts were found more than 50 metres from the nearest path and in areas with sparse ground cover. Coniferous stands were avoided. However, single old spruces within deciduous forest stands were frequently used as sett sites for setts consisting of one or two entrances only. Spruce trees have shallow roots, which facilitate digging and help prevent the roof of the sett from collapsing. Vegetation cover played an important role in the choice of a sett site. However, just "being out of view" (be it through topographic characteristics or distance from the nearest path) could be a type of cover as well. In this study, the small-scale topography around the setts seemed to play a key role in the choice of sett site. The results presented here suggest that a large, deciduous forest with a pronounced topographical variation represents a good badger habitat.

Key words: Meles meles, sett distribution, entrance type, sett site, habitat analysis

# Introduction

In general, carnivores not only show great interspecific diversity in their behavioural ecology (BEKOFF et al. 1984; GITTLEMAN 1986) but also marked intraspecific variability (WILSON 1975). The European badger (*Meles meles* L.) is an example of a species that shows a high degree of plasticity in its behaviour, adapting its social and spatial organisation to

1616-5047/01/66/04-204 \$ 15.00/0.

different environments and food availability. In high-population-density areas with an abundant and highly predictable food availability throughout the year, badgers usually live in groups, defend small territories and occupy distinctive main setts (CHEESEMAN et al. 1981, 1987, 1988; KRUUK 1978; KRUUK and PARISH 1982, 1987; NOLET and KILLING-LEY 1986: RODRIGUEZ et al. 1996: ROPER et al. 1986; WOODROFFE and MACDONALD 1992, 1993). In areas with a seasonally changing, unpredictable food availability, population densities are lower and badgers live in small groups or solitarily, have large overlapping home ranges and use several setts within a range (BOCK 1986; CRESSWELL and HARRIS 1988; GRAF et al. 1996; PIGOZZI 1989; SKINNER and Skinner 1988). Doncaster and Wood-ROFFE (1993) suggested that the spatial organisation of badgers may be influenced by the distribution of suitable sett sites in a given area. Parameters affecting the distribution of badger setts include the type of soil, the amount of cover and the hilliness of the terrain (NEAL 1986). Most assessments of suitable badger setts have been undertaken in mixed wood- and arable land (e.g. CRESS-WELL et al. 1990). These studies showed an active selection for woodland as sett location. However, open fields and meadows were used as foraging grounds and had an important effect on sett choice (HOFER 1988; SKIN-NER et al. 1991).

The goal of this study was to examine sett density, sett type and the specific habitat parameters affecting the distribution of setts in a highly forested habitat (Sihlwald, Switzerland), offering both ideal digging conditions as well as good foraging grounds. Furthermore, the correlation between the distribution of the setts in certain parameter categories and the availability of those categories in the study area was explored.

## Material and methods

#### The study area

The Sihlwald forest is situated approximately 10 km south of the city of Zurich, Switzerland

(47°15' N, 8°34' E). It is characterised by a diverse mosaic pattern ot mixed deciduous forest dominated by beech (Fagus silvatica), with smaller proportions of ash (Fraxinus excelsior), other deciduous trees, white pine (Abies alba) and the introduced Norway spruce (Picea abies). Declared a nature reserve in 1994, it covers approximately 1000 ha of a forested hill chain, ranging from 470 metres a.s.l. at the bottom of the valley to over 900 metres a.s.l. on the ridge. It belongs to the Swiss plateau and consists of subalpine molassic sandstone with partly morrainic cover. The dominant soil types contain sandy to silty clay and argillaceous sand. The extreme relief and well-drained soils make Sihlwald an ideal place for digging setts.

#### Methods

The study area was searched for setts from March until August 1996. A sett was defined as at least one entrance leading more than two metres underground, measured with a two-metre flexible stick. If two entrances were farther than 25 metres apart, they were considered as two separate setts. We assumed that practically all setts were found. The setts were classified into small (1 or 2 entrances), middle-sized (3 or 4 entrances) and large (>4 entrances) setts. Five different entrance types were distinguished: entrances dug directly into the ground, under a boulder/rock, under a spruce (*Picea abies*), under a deciduous tree and under a stump.

This study did not differentiate between fox dens and badger setts for the following reasons. Although it is known that fox dens usually have fewer entrances and a different shape and smell than badger setts (STUBBE 1980), the criteria were not as clear-cut in Sihlwald with dens/setts consisting of one or two entrances that were sporadically used by one or both species. Badger hairs were found in many setts consisting of one entrance only, indicating the presence of badgers in single entrance setts as well. Analysis of sett characteristics based on sett size revealed no statistical difference between setts. Therefore, all setts were included in the habitat analysis presented here. However, to compare main sett density with those in the literature, all setts with more than two entrances and definite badger signs were considered "main setts" (KRUUK 1978). In order to test the distribution of the setts for non-randomness, nearest neighbour distances between the setts were compared with a Monte-Carlo-Simulation of nearest neighbor distances (random distribution, 1000 samples of 123 points) and then tested using a Chi2-test for two independent samples.

The habitat parameters chosen for the analysis are summarised in table 1. The parameters were either measured in the field (field data), or obtained from a Geographical Information System (GIS) using the software ArcInfo, which also contained a digital terrain model of the forest based on 10 metre-contour lines (Tab. 1). The field data were measured within a radius of 25 metres of the approximate centre of the sett. The habitat analysis was calculated by using a stepwise backward logistic regression. The parameters "topography" and "vegetation unit" were used as categorial variables (equivalent to the traditional group of "dummy variables") (NIEVERGELT 1981). The parameters derived from the GIS and the field data could not be analysed together, as the parameters derived from the GIS were available for the whole forest, whereas the field data were available only for the sett sites. For the analysis of the parameters derived from the GIS, a goodness-of-fit test compared the number of observed setts with the number of expected setts for each parameter:

number of expected setts =  $\frac{\text{area of the parameter}}{\text{area of the forest}}$ 

 $\times$  total number of observed setts

To measure the availability of the habitat parameters measured in the field (i.e. the parameters that could not be derived from the GIS database), the number of setts was compared with the number of random points for each parameter by a  $\chi^2$ -test for two independent samples. Due to a strong correlation between "altitude" and "distance to forest boundary", the "distance to forest boundary" was analysed separately. The habitat parameters for which the distribution of the setts was non-random were further analysed to see which categories (Tab. 1) best explain the sett distribution. Every parameter category was tested for deviation from the expected value by using a  $\chi^2$ -test in conjunction with a Bonferroni z statistic (Neu et al. 1974).

## Results

#### Sett size and sett type

123 setts were found in the 1 000 ha study area of Sihlwald (12.3/100 ha). The setts were classified according to entrance number (one to two, three to four, more than four) and entrance types (five classes, see below). Small setts were most common (71.6%), followed by middle-sized (19.5%) and large (8.9%) setts. Using KRUUK's (1978) definition of "main setts" (setts with >2 entrances), the density of main setts in the forest was 3.5/100 ha. The number of entrances per sett varied from one to eleven with an average number of 2.3 entrances per sett. Of the total 279 entrances, 207 (74.2%) were dug into the ground, while the rest were dug under some type of structure (11.1% under spruces, 2.5% under deciduous trees, 7.9% under boulders, 4.3% under tree stumps).

#### Sett spacing

The average nearest neighbour distance between two setts was 111 metres, compared to 158 metres for the average nearest neighbour distance between two generated random points. Thus, the observed distribution of the setts was significantly different from random ( $\chi^2$ -test for two independent samples, p < 0.001).

When the nearest neighbour distance was calculated for the "main setts" only, the average nearest neighbour distance was 311 metres, compared to the 314 metres for the average nearest neighbour distance between two generated random points. The distribution of "main setts" did not differ from random.

#### Habitat analysis of the setts

The results of the stepwise backward logistic regression show that sett sites were positively associated with the parameters "convex slope", "inclination" and "distance to nearest path" but negatively associated with "concave slopes", "flat areas", "gentle slopes", as well as "moss-", "herb-" and "middle layer coverage" (Tab. 2). The results for the different parameter categories are as follows:

Forest parameters and vegetation cover: The forest parameters and vegetation cover seemed to play a key role. The results showed that the parameters of the setts differed significantly from the availability of those parameters for "lower layer cover-

Parameter	Subscales	Categories	Source of data
Sett location	X-coordinates Y-coordinates	continuous	Field data
Altitude	metres a.s.l.	≤ 600 m; ≤ 700 m; ≤ 800 m; > 800 m	GIS
Inclination	degrees	0–10°; 11–20°; 21–30°; 31–40°; > 40°	Field data
Aspect	degrees	N; NE; E; SE; S; SW; W; NW	GIS
Topography*	flat gentle slope concave slope convex slope crest		Field data
Vegetation cover	tree cover (> 1.3 m) shrub cover (0.5–13 m) herb cover (0–0.5 m) moss cover	BRAUN-BLANQUET (1964): 0, 1–5%, 6–25%, 26–50%, 51–75%, > 75%	Field data
Forest parameters**	lower-, middle and upper layer coverage	Braun-Blanquet (1964): 0, 1–5%, 6–25%, 26–50%, 51–75%, >75%	GIS
	lower-, middle- and upper coniferous layer coverage	BRAUN-BLANQUET (1964): 0, 1–5%, 6–25%, 26–50%, 51–75%, >75%	GIS
	vegetation unit		GIS
	stage of development	1 = young growth; 2 = pole wood; 3 = young timber wood; 4 = middle timber wood; 5 = old timber wood I; 6 = old timber wood II; 7 = old timber wood III	GIS
Distance to nearest path	metres	≤ 50 m; ≤ 100 m; ≤ 150 m; ≤ 200 m; > 200 m	GIS
Distance to nearest water	metres	$\leq$ 50 m; $\leq$ 100 m; $\leq$ 150 m; > 150 m	GIS
Distance to forest boundary	metres	$\leq$ 100 m; $\leq$ 200 m;; $\leq$ 900 m; > 900 m	GIS

 Table 1. Habitat parameters for setts. The parameters were either measured in the field (field data), or were obtained from the Geographical Information System (GIS)

\* gentle slope: a slanting surface neither curving inward nor outward concave slope: a slope curving inward convex slope: a slope curving outward, like a segment of a globe.

\*\* data from the forest superintendent's office (Waldamt der Stadt Zürich). lower layer coverage density: canopy density that reaches at most 1/3 of the dominant tree height. middle layer coverage density: canopy density that reaches 1/3–2/3 of the dominant tree height. upper layer coverage density: canopy density that reaches at least 2/3 of the dominant tree height.

age" and "lower-" and "middle coniferous layer coverage" (Tab. 3 a). However, more setts than expected were found only in areas lacking a "middle coniferous layer coverage" (Tab. 4; Bonferroni z statistic, p < 0.05). The parameters of the setts differed significantly from the random points for herb- and moss coverage (Tab. 3 b;  $\chi^2$ test for two independent samples, p < 0.05 and p < 0.01, respectively), as setts were more frequently found in areas with little "herb-" and no "moss coverage" (Tab. 4; Bonferroni z statistic, p < 0.05 and p < 0.01 respectively).

Habitat parameter	В	df	p-value
Inclination	0.0695	1	0.0006
Topography flat gentle slope concave slope convex slope	-0.6172 -0.2514 -1.5706 0.8271	4	0.0247 0.6818 0.8821 0.1194 0.3550
Distance to nearest path	0.0144	1	0.0006
Middle layer coverage	-0.0288	1	0.0486
Herb coverage	-0.3226	1	0.0351
Moss coverage	-0.8196	1	0.0053

**Table 2.** Habitat parameters that best explain the occurrence of the setts. Multiple logistic regression (backward, stepwise), Model- $\chi^2$  = 92.36; df = 10; p < 0.001; R<sup>2</sup> = 0.77

**Table 3.** Comparison of the habitat parameters of the setts derived from the GIS with the availability of those parameters within the study area (a); comparison of the habitat parameters of the setts with those of the random points (b). Only the parameters for which the distribution of the setts is significantly non-random are listed here. Goodness-of-fit test; df = degrees of freedom. For (b):  $n_1 = 123$ ;  $n_2 = 85$ 

a) Comparison with availability	p-value	χ²	df	
Altitude	p < 0.001	128.23	3	
Aspect	p < 0.02	16.78	7	
Lower layer coverage	p < 0.02	12.69	4	
Lower coniferous layer coverage	p < 0.005	12.39	2	
Middle coniferous layer coverage	p < 0.02	10.89	3	
Distance to forest boundary	p < 0.05	17.61	9	
Distance to nearest path	p < 0.001	18.10	3	
Distance to nearest water	p < 0.05	10.82	4	
b) Comparison with random points	p-value	χ <sup>2</sup>	df	
Inclination	p < 0.001	52.41	4	
Topography	p < 0.001	40.04	4	
Herb coverage	p < 0.05	19.63	5	
Moss coverage	p < 0.01	15.44	2	

Inclination and topography: Comparison of the habitat parameters of the setts measured in the field with those of the random points (Tab. 3 b) showed that setts differed significantly from random points for "inclination" and "topography" (both:  $\chi^2$ -test for two independent samples, p < 0.001). "Convex slopes" with the inclination categories  $\leq 30^\circ$  and  $\leq 40^\circ$  were significantly preferred sett sites (Tab. 4; Bonferroni z statistic, p < 0.001).

Distances to forest boundary, forest roads and trails, and water: The distribution of the setts was decidedly non-random for these three parameters (Tab. 3 a). Setts are found significantly closer ( $\leq 100$  m) to the forest boundary than expected (Tab. 4; Bonferroni z statistic, p < 0.05). Significantly more setts than expected were found  $\geq 50$  m but  $\leq 100$  metres to the nearest road or trail (Tab. 4; Bonferroni z statistic, p < 0.001). No difference was obtained for any category of the parameter "distance to nearest water". Altitude and aspect: The distribution of the setts was non-random for "altitude" (Tab. 3 a;  $\chi^2$ -test for two independent samples, p < 0.001) as well as for "aspect" (p < 0.02). More setts were found

_
a a
2
<u>.</u>
ٽ <u>ب</u>
1
8
Ĕ
ā
Ť
i
4
5
0
0
2
5
S
2
5
E C
st
·
0
•
5
0
5
<u> </u>
ā
·
t
S
5
<u> </u>
Ħ
Ū.
Š
-
5
Ŧ
Ú
e.
Ŧ
en e
-
2
Ū
Š
10
·
S
0
0
S
ίΰ.
۰Ē
ā
Ĕ.
ai'
4
ίσ
U
1
e
÷.
ē
E
ā
2
co.
b
-
E
ш
can
fican
ifican
nifican
gnifican
ignifican
significan
ll significan
all significan
r all significan
or all significan
for all significan
) for all significan
4) for all significan
74) for all significan
974) for all significan
1974) for all significan
1974) for all significan
., 1974) for all significan
ıl., 1974) for all significan
al., 1974) for all significan
t al., 1974) for all significan
et al., 1974) for all significan
u et al., 1974) for all significan
EU et al., 1974) for all significan
NEU et al., 1974) for all significan
(NEU et al., 1974) for all significan
l (NEU et al., 1974) for all significan
all (NEU et al., 1974) for all significan
vall (NEU et al., 1974) for all significan
rvall (NEU et al., 1974) for all significan
ervall (NEU et al., 1974) for all significan
itervall (NEU et al., 1974) for all significan
Intervall (NEU et al., 1974) for all significan
Intervall (NEU et al., 1974) for all significan
e Intervall (NEU et al., 1974) for all significan.
ice Intervall (NEU et al., 1974) for all significan
nce Intervall (NEU et al., 1974) for all significan
lence Intervall (NEU et al., 1974) for all significan
idence Intervall (NEU et al., 1974) for all significan
fidence Intervall (NEU et al., 1974) for all significan
ufidence Intervall (NEU et al., 1974) for all significan
onfidence Intervall (NEU et al., 1974) for all significan
Confidence Intervall (NEU et al., 1974) for all significan
i Confidence Intervall (NEU et al., 1974) for all significan
ii Conf
ii Conf
roni Conf
roni Conf
erroni Conf
erroni Conf
roni Conf
onferroni Conf
nferroni Conf
. Bonferroni Conf
onferroni Conf
4. Bonferroni Conf
4. Bonferroni Conf
4. Bonferroni Conf
ble 4. Bonferroni Conf
able 4. Bonferroni Conf
ble 4. Bonferroni Conf
able 4. Bonferroni Conf

Parameter	Category	Availability	Demand	Estimate	Estimate in %	Lower c. i.	Upper c. i.	Bonferroni parameters	p-value
Middle coniferous layer coverage	0	55.35	69	55.193	0.4487	0.4492	0.6727	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 10.92$ p < 0.01
Herb coverage	1-5%	11	30	15.733	0.1279	0.1417	0.3461	n = 6; p = 0.05; z = 2.6383	$\chi^2 = 43.17$ p < 0.05
Moss coverage	0	51	100	72.942	0.5930	0.7252	0.9008	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 27.01$ p < 0.001
Inclination	≤ 30%	14	53	20.259	0.1647	0.3159	0.5459	n = 5; p = 0.05; z = 2.5758	$\chi^2 = 125.85$ p < 0.001
	≤ 40%	2	23	7.235	0.0588	0.0964	0.2775	n = 5; p = 0.05; z = 2.5758	$\chi^2 = 125.85$ p < 0.001
Topography	convex slope	12	62	17.163	0.1395	0.3879	0.6202	n = 5; p = 0.05; z = 2.5758	$\chi^2 = 144.17$ p < 0.001
Distance to forest boundary	≤ 100 m	œ	24	11.576	0.0941	0.0948	0.2954	n = 10; p = 0.05; z = 2.8071	$\chi^2 = 55.23$ p < 0.05
Distance to path	≤ 100 m	33.33	47	33.331	0.2710	0.2727	0.4915	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 18.19$ p < 0.001
Altitude	≤ 700 m	23.4	45	23.402	0.1903	0.2574	0.4743	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 128.23$ p < 0.001
	≤ 800 m	12.03	28	12.031	0.0978	0.1332	0.3221	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 128.23$ p < 0.001
	> 800 m	0.02	10	0.020	0.0002	0.0198	0.1428	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 128.23$ p < 0.001

A habitat analysis of badger (Meles meles L.) setts

209

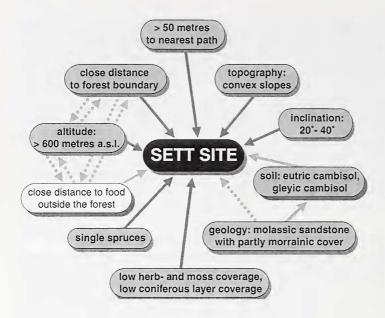


Fig. 1. Parameters positively affecting sett site in Sihlwald. Grey ovals: parameters measured in this study or taken from available data sets for the study area. White ovals: parameters that are difficult to assess but probably influence the choice of sett sites. Arrows indicate the interrelations between the parameters.

>600 metres a.s.l. (Tab. 4; Bonferroni z statistic, p < 0.001). No significant difference was obtained for any category of "aspect" other than North, for which fewer setts than expected were found (Tab. 4; Bonferroni z statistic, p < 0.05). Figure 1 illustrates the different parameters positively affecting sett sites in Sihlwald.

# Discussion

#### Sett size and sett type

The number of entrances per sett in Sihlwald, ranging from one to eleven, was well below the average found in the literature (1 to 21: KRUUK 1978; 1 to 38: ANRYS and LIBOIS 1983; 1–80: ROPER 1992 a, b), even compared to that of the other studies in Switzerland (1–28: GRAF et al. 1996; 1 to 15: FERRARI 1997; 2–23: MONNIER, unpublished data; 1–34: DOLINHSAN, unpublished data). Badgers seem to prefer burrowing more setts but with fewer entrances in the forest than in the agriculture zone where sett sites are restricted to the little patches of forest between the agricultural fields and meadows (DOLINHSAN, unpublished data). We suggest that badgers living in Sihlwald can optimise their foraging efficiency by using different setts within their home range according to the proximity of the seasonally most profitable food patches. Future analysis of the seasonal sett-use together with seasonal variations in foraging behavior in the study area will provide the necessary data to test this hypothesis.

In Sihlwald, 28.4% of the setts found showed more than two entrances and could indicate main setts (KRUUK 1978). However, their distribution did not differ from random and therefore did not show a spacing-out mechanism indicating territories according to the fixed-territory model proposed by DONCASTER and WOODROFFE (1993) for a high-density badger population.

With regard to the entrance types, it is surprising that 31 entrances (11%) were dug under relatively large spruces. Although sett locations have been analysed in several studies, only BOCK (1986) classified different sett types. However, his study did not mention anything about setts dug under spruces. The spruces in Sihlwald were all in mixed forests. A possible explanation is that spruce trees are normally shallow rooted (KÖSTLER et al. 1968; BLANCKMEISTER and HENGST 1971), compared to the dominant beech trees in Sihlwald. Shallow roots facilitate digging; also the roots keep the roof of the sett from collapsing. It is also of interest to note that 22 entrances (7.9%) were dug under a boulder/rock. To our knowledge, single rocks as a possible habitat parameter for sett location, providing shelter and good thermal insulation has only been mentioned in one other study (VIRGOS and CASANOVAS 1999).

#### Cover as key factor

The habitat parameters affecting the distribution of setts in Sihlwald correspond closely to those identified by NEAL (1986) and THORNTON (1988): digability, hilliness and (tree-) cover. Cover allows the badgers to leave inconspicuously, and it allows the young cubs to play near the entrance without being visible to potential predators. A closer look at the vegetation cover around the preferred sett sites in Sihlwald shows that these sites are areas of sparse ground cover (i.e. low herb- and moss coverage). High herb and moss coverage often is correlated with humidity and therefore avoided by badgers as sett sites. As observed in other studies (NEAL 1986; ZEJDA and NESVADBOVA 1983), coniferous stands providing little vegetation cover and found in rather flat areas were avoided in Sihlwald. The preference for convex slopes with a high inclination (20-40°) as well as the preference for a minimum distance of 50 m from the next path suggest that the variable "cover" is not necessarily equivalent to vegetation cover; the small-scaled topography around the sett and the distance to the nearest path (just "being out of view") can indirectly be a type of cover as well. Topography, i.e., the physical shape of the area in which a sett is dug, is a parameter that has never been stressed in the literature before and seems to play a key role in the choice of sett site in Sihlwald. Paying attention to the small-scale topography  $(\emptyset 50 \text{ metres})$  around the sett appears to be important. Setts dug in convex slopes

have several advantages. The badger can pick up scents from different directions without having to leave the security of the sett and thus have several directions from which to leave a sett. It is also possible that setts on convex slopes are easier to enlarge because the rounded shape of the slope gives the badgers more opportunities for digging entrances and connecting tunnels than an unstructured slope. Inclination ("hilliness" according to THORNTON 1988) is also closely associated with topography. Setts are usually dug in slopes (NEAL 1986; SKINNER et al. 1991). The hilliness of the study area is advantageous to the badger in various ways. Digging in a slope facilitates the removal of the excavated soil, which spills down the slope. A particularly favourable stratum of soil for digging is more easily found on a slope since it is more likely to be exposed. Sloping land is usually well drained so that the sett is more likely to be warm and dry, and in colder parts a depth below ground is quickly attained which is frost free (NEAL 1986).

#### Sett density and population density

The density or setts in Sihlwald (12.3/ 100 ha) is very high compared to the density of the nearby agricultural zone (2.7/ 100 ha, DoLINHSAN, unpublished data). This implies that suitable sett sites are not a limiting factor in the forest, as suggested by ROPER (1993) for British areas. Other regions of Switzerland (Canton of Neuchâtel: 0.02–0.2/100 ha. MONNIER, unpublished data: Canton of Berne: 4.2/100 ha. GRAF et al. 1996) have also lower sett densities. Still, Sihlwald has a significantly lower sett density than found in Britain (up to 26/100 ha, CRESSWELL et al. 1990). The density of possible main setts in Sihlwald (3.5/100 ha) is comparable to that in the high-badger-density areas in Britain (CLEMENTS et al. 1988, see Kowalczyk et al. 2000, for review). Based on the available earthworm biomass, which is the most important food source for badgers in Sihlwald, the minimum population size is estimated to be 2.5 to 3 individuals per 100 ha (HINDENLANG, unpub-

lished data). Therefore, also the badger density in Sihlwald is high compared to the published densities across Continental Europe, but, in contrast to the main sett density, lies much lower than the estimated population densities of the British Isles (KOWALCZYK et al. 2000). KOWALCZYK et al. (2000) showed that log densities of badger setts correlate negatively with the percent forest cover in the area. This is certainly not the case in Sihlwald where forest covers approximately 70% of the area used by badgers living in the Sihlwald (pers. observation). In the nearby agricultural zone with a much lower sett density forest covers approximately 17% of the area. We argue that this high sett density and considerably high badger density in Sihlwald is attained through a combination of ideal sett-site conditions as well as a rich and varied food supply. According to the literature, a mixture of woodland and pastures, and woodland and arable land is among the habitat types preferred by the badger (BROSETH et al. 1997; Hofer 1988; Neal 1977; Zedja and NESVADBOVA 1983). Also, the setts in Sihlwald are found significantly closer to the forest boundary and adjoining agricultural zones than random points. Other studies have noted that badger setts tend to be situated close to habitat edges, i.e. on boundaries between two habitat types (O'CORRY-CROWE et al. 1993; VIRGOS and

CASANOVAS 1999). The proximity of setts to the forest boundary and adjoining agricultural zones makes access easier to an optimal food supply year-round without forfeiting optimal sett sites that the forest offers with its pronounced topography. The diverse pattern of mixed deciduous forest stands in Sihlwald itself contains good worm patches even in dry periods (HINDEN-LANG, unpublished data). Badgers can therefore adapt their foraging to the seasonal changes in food availability, both within the mixed forest stands and in the agricultural fields and meadows outside the forest. We suggest that the spatial organisation of badgers living in the Sihlwald area is primarily determined by the seasonal availability of food resources.

# Acknowledgements

We thank GERULF RIEGER and WERNER SUTER for the helpful comments on the drafts. Furthermore, we would like to thank LORENZ GYGAX and WOLF BLANKENHORN for the statistical advice and SU-SANNE REIMANN for helping us draw figure 1. We are also very indebted to all those who helped us find numerous setts. K. HINDENLANG was supported by the Swiss National Fund ("Adjustment of spatial behaviour of European badger (*Meles meles* L.) in response to a heterogeneous environment", Nr. 3100-40846.94/3100-52988.97).

# Zusammenfassung

# Eine Analyse der Habitatcharakteristika von Dachsbauen (*Meles meles* L.) in einem naturnahen Wald

Größe, Verteilung und Habitatcharakteristika von Dachsbauen wurden in einem naturnahen Wald untersucht. Die Verteilung der Dachsbaue im Untersuchungsgebiet war nicht zufällig, wobei jeweils die Distanzen zum nächst benachbarten Bau mit den Distanzen zu Zufallspunkten verglichen wurden. Für die Bestimmung der charakteristischen Habitatfaktoren, die die Verteilung der Baue im Untersuchungsgebiet erklären, wurden verschiedene Kategorien von Habitatparametern für Topographie, Vegetation und Struktur des Waldhabitats mittels Multipler Regressions-Analyse und mithilfe eines digitalen Geländemodells in einem Geographischen Informations-Systems (GIS) analysiert. Bevorzugte Standorte waren konvexe Hangrippen mit einer Inklination zwischen 20° und 40°. Sie sind gut entwässert und bieten dem Dachs die Möglichkeit, Baueingänge und -röhren zu graben, die ein Verlassen des Baus und das Aufnehmen von Witterung aus verschiedenen Himmelsrichtungen erlauben. Bevorzugte Standorte für Dachsbaue befanden sich in Höhenlagen über 600 Meter ü. M. sowie näher am